

First fossil record of a finfoot (Aves: Heliornithidae) and its biogeographical significance

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Abstract.—The distal end of a humerus from the Lee Creek Mine in North Carolina is identified with the modern Neotropical species as *Heliornis* aff. *fulica* and provides the first fossil record for the family Heliornithidae. The fossil was determined to come from the Middle Miocene (14 Ma) Pungo River Formation based on sedimentary, preservational, and other lines of evidence. This in turn implies that *Heliornis* did not spread into South America until after the isthmian land connection about 3 Ma and that the interchange of Heliornithidae between the Old and New World probably took place through the Northern Hemisphere in the Paleogene.

The finfoots or sungrebes (Heliornithidae) comprise 3 species, each in a monotypic genus, that are placed in the traditional avian order Gruiformes. On the basis of both morphology and molecular data, the family is probably most closely related to rails, Rallidae (Houde 1994, Livezey 1998). The species are sedentary, swimming and diving birds of forested streams in the tropics of the New World, Africa, and southeast Asia. Hitherto, there has been no fossil record of the family (Brodkorb 1967, Houde 1994, Tommy Tyrberg, Kimstadt, Sweden, pers. comm.). This has changed with the discovery of the distal end of a humerus in spoil piles of the Lee Creek phosphate mine near Aurora, North Carolina, from which tens of thousands of fossil bird bones had been recovered previously (Olson and Rasmussen 2001).

Systematics

Class Aves

Order Gruiformes

Family Heliornithidae

The fossil humerus is characterized by its short, curved overall shape, which at first suggests a medium-sized species of one of

the “higher” orders of arboreal land birds (Olson 1985). It differs from all of these in the very rounded, hemispherical condylus ventralis (ulnar condyle), which contrasts markedly with the narrow, transversely ovoid, and often proximally flattened condyle in the traditional orders Coliiformes, Trogoniformes, Coraciiformes, Piciformes, and Passeriformes. Another highly distinctive character is the extension of the epicondylus ventralis distally well past the margins of the distal condyles. These two features (Fig. 1) in combination with the overall size and shape are diagnostic of the Heliornithidae.

Genus *Heliornis* Bonnatere, 1791

There is little in the way of qualitative differences in the distal half of the humerus to distinguish the three genera of Heliornithidae. *Podica* and *Heliopais* differ from *Heliornis* and the fossil in their much larger size, so that on size and geographical grounds it is more reasonable to assign the fossil to the type-genus of the family, *Heliornis*.

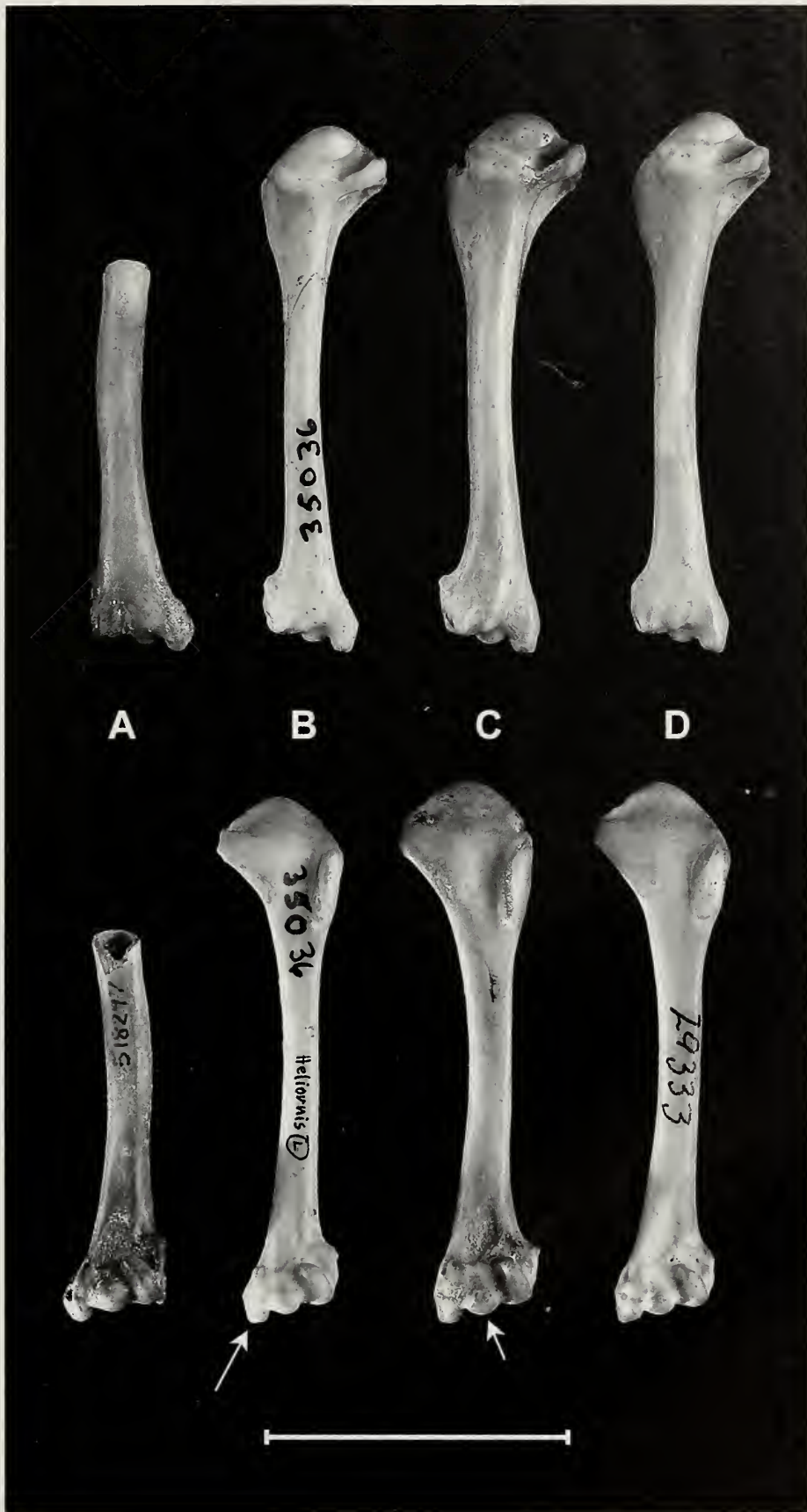


Fig. 1. Left humeri of *Heliornis* (top row anconal view; bottom row palmar view): A, fossil *Heliornis* aff. *fulica* from Lee Creek Mine, North Carolina; B, C, modern *Heliornis fulica* (UF 38828 = PB 35036; USNM 321493; UF 33412 = PB 29333). The distally projecting epicondylus ventralis (long arrow) and the very rounded, hemispherical condylus ventralis (short arrow) are diagnostic features of the Heliornithidae.

Table 1.—Measurements (mm) of the humerus of modern *Heliornis fulica* (Heliornithidae) compared with fossil humerus of *Heliornis* aff. *fulica* (USNM 518297) from the Miocene of North Carolina.

	<i>Heliornis fulica</i> (N = 13) Range (mean) SD	<i>Heliornis</i> aff. <i>fulica</i> fossil
Distal width	6.2–7.0 (6.8) 0.24	6.9
Shaft width	2.4–3.2 (2.8) 0.19	3.2
Shaft depth	2.4–2.8 (2.6) 0.12	2.9

Heliornis aff. *fulica* (Boddaert, 1783)

Referred specimen.—Distal half of left humerus, National Museum of Natural History, Smithsonian Institution, USNM 518297, collected 13 June 2001 by Geoff Keel.

Locality.—Lee Creek Mine, south side of Pamlico River, near Aurora, Beaufort County, North Carolina (35°23'22"N, 76°47'06"W).

Horizon.—Pungo River Formation, Middle Miocene; Langhian stage, ca. 14 Ma (Gibson 1983). Fossil birds at the Lee Creek Mine come from deposits of two ages separated by an unconformity—the Middle Miocene Pungo River Fm and the Lower Pliocene Yorktown Fm (Olson and Rasmussen 2001). Assignment of the present fossil is based on several lines of evidence. It was recovered from a spoil pile that was topped by sediments of the Pungo River Fm; the preservation is excellent, the bone having a hard, shiny surface, unlike the etched appearance of many of the bones from the Yorktown Fm; blackish phosphatic sand characteristic of the Pungo River Fm was adherent to the fossil; and no strictly tropical elements occur in the Yorktown Fm but are known from the Pungo River and equivalent formations.

Comparisons.—In size, the fossil falls within the range of modern *Heliornis fulica* in two measurements, though near the high end, and is very slightly larger in shaft depth (Table 1). Although the shaft of USNM 518297 is thus generally somewhat more robust, this character varies consid-

erably in the modern series. Qualitatively, the only apparent differences are the somewhat more curved shaft, the relatively larger condylus ventralis, and the wider sulcus musculo humerotricipitalis in the fossil. These differences may indicate slight differences in flight capability, but given the time disparity they are very minor. There is nothing in this single fossil to suggest that it represents a divergence from the lineage leading to the modern species *Heliornis fulica*. This perception might be altered if more of the skeleton were available.

Discussion

The Heliornithidae are among the classic examples pantropical families of birds (Fig. 2), such as barbets (Capitonidae) and trogons (Trogonidae), which likewise occur in the Old and New World tropics, but not in Australasia. This pattern invites the question of whether their distribution is the result of vicariant events or dispersal.

Modern *Heliornis fulica* extends practically throughout the Neotropics from Mexico to northern Argentina. The fossil record from North Carolina is more than 2600 air line km NE of the nearest occurrence of *Heliornis* in Veracruz, Mexico. The specimen comes from deposits about 14 Ma, whereas a land connection was established between North and South America only about 3 Ma, with mammalian overland dispersal having taken place in both directions before about 2.5–2.8 Ma (Marshall 1985).

Finfoots, being weak fliers and with very specific aquatic habitat requirements, are almost certainly incapable of dispersing over an oceanic barrier. Thus, the evidence now at hand suggests that *Heliornis fulica* must have spread into South America from North America after the isthmian land connection formed, and perhaps considerably after that, given that it has no recognized subspecies (Hellmayr and Conover 1942).

Heliornis differs from other finfoots in having altricial young that are carried in axillary marsupia (Houde 1994), so that it is



Fig. 2. Modern distribution of the three species of Heliornithidae (solid) and the only fossil record (arrow). Map modified from Fisher and Peterson (1964).

presumably the most derived of the three species. Houde (1994) found *Heliornis* to be closer genetically to the Asian genus *Heliopais*, than to the African genus *Podica*, although the quality of the DNA of *Heliopais* may have been equivocal. He also found that the degree of genetic divergence between *Heliornis* and the African genus *Podica* was too small to be compatible with a trans-Atlantic origin of the former and subsequent separation via sea-floor spreading, which would have necessitated a common distribution across what is now Africa and South America well back into the Cretaceous (Smith et al. 1994).

Assuming finfoots to require tropical environments and to be incapable of crossing marine water barriers, interchange of finfoots between the Old and New World must have taken place early in the Tertiary across the Northern Hemisphere, because *Heliornis* was already in North America by the Middle Miocene. There is abundant floral and faunal evidence for interchange between North America and both Europe and Asia in the Eocene (Manchester 1999) and in particular for invasions of mammals from Asia in the late Eocene (Woodburne

and Swisher 1995). Thus, fossils of Heliornithidae might be anticipated in Paleogene deposits of the northern continents.

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